

# ON THE TAXONOMY AND DISTRIBUTION OF VACCINIUM ULIGINOSUM

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The tundra bilberry, *Vaccinium uliginosum* L. is a characteristic shrub of tundra and muskeg in boreal, arctic and alpine regions. The species has a circumpolar range (Fig. 1) which extends southward into the temperate zone in coastal regions and mountainous areas.

Various morphological and cytological features of the *V. uliginosum* complex have been discussed by a number of authors, including Fernald (1923), Petersen (1933), Hagerup (1933), Malte (1934), Hara (1953), Young (1965, unpub.), Löve and Löve (1966), and D. Löve and Boscaiu (1966). Most of these treatments refer to certain circumscribed geographical areas, and the methods used to distinguish races within these areas have often proved to be unworkable when applied on a broader scale. There is a great deal of morphological variation within the complex, but much of this variation is quantitative rather than qualitative: few clearcut morphological discontinuities are to be found. An additional complication results from the wide range of ecological tolerance found in some populations of *V. uliginosum*. These populations show much variation in leaf size, growth habit, phenology, and other characters. Much of this variation seems to be ecologically induced. Lack of information on the breeding systems and on the genetic structure of the races of *V. uliginosum* further complicates the situation.

In spite of these difficulties, there are a number of clearcut patterns of morphological variation which can be discerned when the *V. uliginosum* complex is treated on a circumpolar, holarctic scale. These patterns are correlated with distributional and cytological data. They allow the delineation of a series of distinct, wide ranging races within the *V. uliginosum* complex. Most of these races intergrade more or less freely in zones of range overlap, even though

they may differ cytologically. Therefore, the races are here treated as subspecies, at least one of which can be further subdivided into two varieties.

#### CYTOLOGY

At least three levels of a euploid sequence based on  $n=12$  have been found in *V. uliginosum*. The collection locations of specimens from which chromosome counts have been made are shown in Fig. 1.

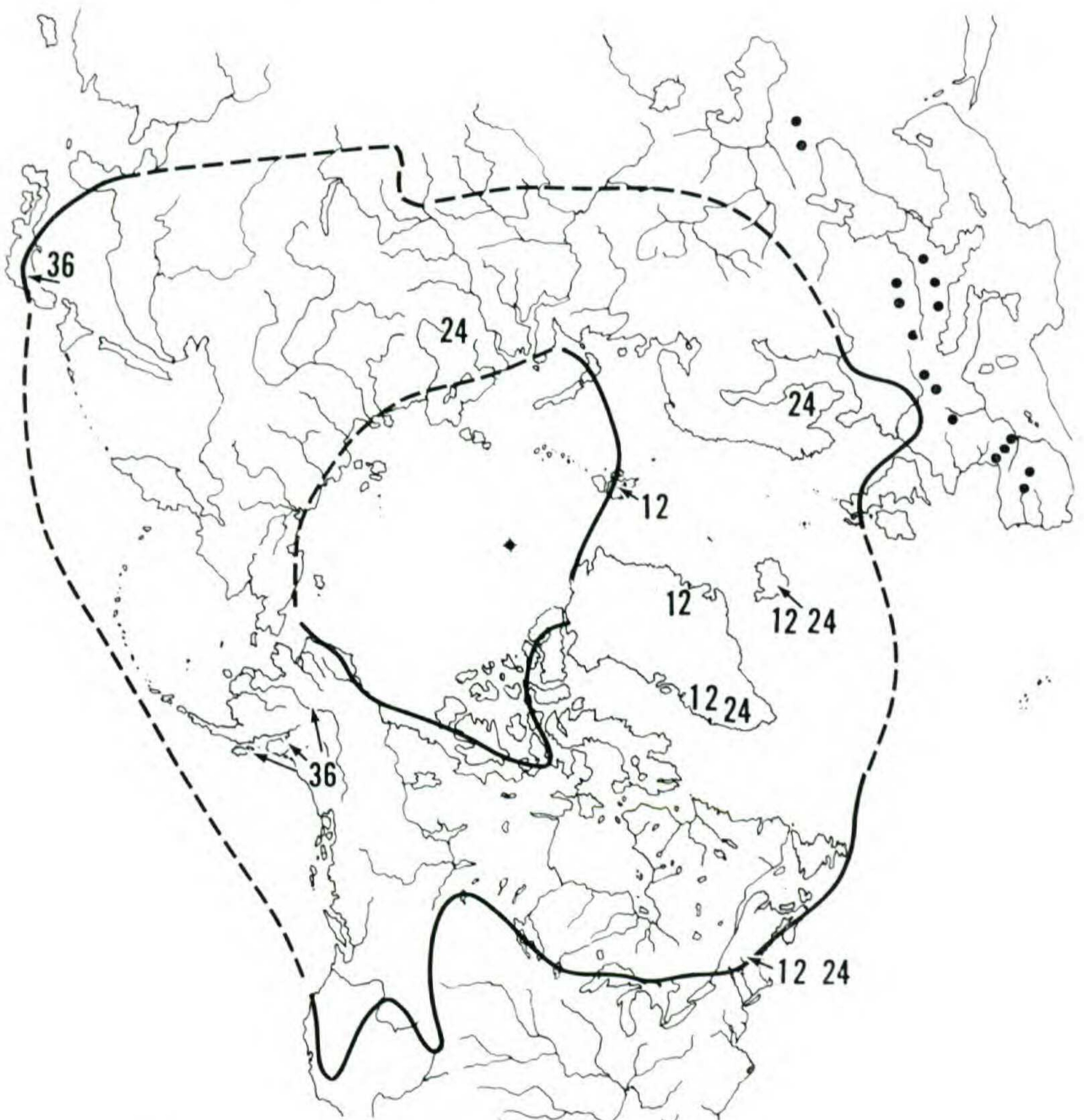


Fig. 1. Outline of the range of *Vaccinium uliginosum* s. lat. Dots indicate isolated alpine stations in Europe. The numbers indicate documented chromosome counts and the locations at which the specimens were collected.

Documented chromosome counts of  $n=12$  (diploid) have been obtained from Greenland (Hagerup, 1933, Jorgensen, et al, 1958), Spitzbergen (Flovik, 1940), Iceland (Löve, 1950, 1954), and Mount Washington, New Hampshire (Löve and Löve, 1966).

Counts of  $n=24$  have been made from Greenland (Hagerup, 1933, Jorgensen et al, 1958), Iceland (Löve, 1954, Löve and Löve, 1956), Sweden (Hedberg and Hedberg, 1964), and arctic Russia (Sokolovskaya and Strelkova, 1960).

Counts of  $n=36$  are reported from alpine areas in Honshu, Japan (Hara, 1953), and from a number of stations in central and southern Alaska (Young, 1965, unpub.).

In the course of an earlier study on *V. uliginosum* in Alaska (Young, 1965, unpub.), I made over 100 slides of meiotic material of *V. uliginosum* from many stations in Alaska. I was able to obtain counts from 10 stations which I was reasonably satisfied represented exactly  $n=36$ . However, the majority of the counts showed anomalous numbers. In many cases it was clear that there were more than 24 but less than 36 chromosomes, while in a few cases the number appeared to exceed 36. One slide made from material from an alpine station on Kodiak Island seemed to show  $n=18$ , while material from nearby stations was often clearly  $n=36$ .

Chromosomes of Alaskan material of *V. uliginosum* are small and "sticky." Stages of meiosis suitable for counting are difficult to find, and cytoplasmic staining is often a problem. Therefore, it is difficult to get a perfectly accurate count, particularly when the chromosomes are numerous. However, there can be no doubt that many Alaskan specimens of *V. uliginosum* have a chromosome complement that is anomalous in terms of the normal sequence based on  $n=12$ . A similar situation has been described by Lewis (1970) in populations of *Claytonia virginica* L. in Texas. It was found that chromosome numbers in these populations varied between individuals within populations, between various organs of individual plants, and, in terms of average numbers, throughout the population as a whole over

a period of time. The latter phenomenon apparently was correlated with climatic stress (drought in that case). It seems likely that there is a similar situation of "Chromosomal Drift" in many Alaskan populations of *V. uliginosum*. The significance of this situation with respect to fertility and breeding systems is not clear. It seems likely that the great amount of morphological variability observed in central Alaskan populations of *V. uliginosum* is correlated with a complex genetic structure of the populations, and that variations in chromosome numbers are an aspect of this complexity. It is unfortunate that the relatively long life cycle of *V. uliginosum* militates against using the species in hybridization studies.

#### MORPHOLOGY AND TAXONOMIC CRITERIA

In approaching the taxonomy of *V. uliginosum* on a holarctic scale, leaf pubescence and growth habit of the plant are the most useful morphological characters. These characters also show good correlations with distributional data, and there are many areas in which all populations of *V. uliginosum* seem to be quite uniform in terms of these characters. Areas in which there is more variation in leaf pubescence and growth habit are apparently zones of contact and intergradation between two or more races. In the case of growth habit, there is often considerable variation in geographically complex areas such as central Alaska; this variation must, to some extent, be ecologically induced.

A third character of major significance is the presence or absence of stomates on the upper surface of the leaves. This character is easily determined on herbarium specimens, using the plastic imprint technique described by Sinclair and Dunn (1961). The presence or absence of stomata on the upper surface of the leaves is the only character I have found that allows a race of *V. uliginosum* to be distinguished in all cases.

Several of the characters which earlier workers have considered to be useful in distinguishing races of *V. uliginosum* seem to be of little value when applied on a holarctic

scale. Variation in the length and angle of divergence of anther horns has been considered to be significant by a number of workers. Short, ascending anther horns were thought by Hagerup (1933) to be useful in distinguishing tetraploid plants in Greenland from their long-horned diploid counterparts. Short, even obsolete anther horns occur commonly in most populations of *V. uliginosum* from the more temperate parts of the range, but in no case does their occurrence seem to be universal throughout a population.

Size, shape, and color of the corolla, mean number of carpels, length of pedicels, and the number of flowers per inflorescence all vary somewhat between the major races of *V. uliginosum*. In no case is the variation in any one of these characters great enough to use it as a diagnostic taxonomic character.

D. Löve and Boscaiu (1966) indicate that *V. gaultherioides* (here treated as *V. uliginosum* ssp. *gaultherioides*) can be distinguished from *V. uliginosum* s. str. on the basis that *V. gaultherioides* lacks small, stalked glands along the margin of the base of the leaf. In all of the several hundred specimens of *V. uliginosum* s. lat. that I examined, I found none in which these glands did not occur on at least some of the leaves. The glands are most noticeable on young leaves and tend to wither on older leaves.

Narrow-leaved individuals occur in most races of *V. uliginosum*, but they are most commonly found in populations in northwestern North America. Individuals with narrow leaves have sometimes been given taxonomic status (e.g. *V. salicinum* Cham.). However, these individuals seem to occur randomly in otherwise normal populations, and they are of little or no taxonomic significance.

Fruit characters are of little use in the taxonomy of *V. uliginosum*, partly because the shape and size of the fruits are difficult to determine from pressed specimens. Fruits of ssp. *pedris* are quite variable in shape (c.f. Shacklette, 1962), while those of other races are normally spherical. There is apparently considerable variation in the sugar con-

tent and palatability of the fruits between races (Harshberger, 1928, Hagerup, 1933).

Porsild (1951) claimed that there are two races of *V. uliginosum* in northwestern Canada. These races are supposedly distinguishable on the basis that one has fruits with persistent, "capitate" styles, while the other has deciduous "continuous" styles. The styles of most specimens of *V. uliginosum* exude a drop of a resinous substance at the tip at about the time of anthesis, perhaps as a pollen trapping mechanism. This exudate hardens into an acellular globule at the end of the style at the same time that the style is withering and diminishing in diameter. The result is a "capitate" style, which occurs on all *V. uliginosum* specimens with mature fruit that I have studied. The style is usually jointed at the base and easily broken off when the fruits are mature. I have seen no specimens in which the presence or absence of the style on the fruit can be considered to have taxonomic significance.

#### CORRELATION BETWEEN MORPHOLOGICAL AND CYTOLOGICAL DATA

A major problem in the taxonomy of the *V. uliginosum* complex has involved attempts to correlate morphological characters with cytological data. In East Greenland and northern Europe there are fairly clear cut morphological and habitat-preference separations between the two common races of the complex. There is sufficient data to indicate that procumbent, small-leaved populations growing in dry situations in arctic areas are diploid, while tall, large-leaved hydrophytes from more temperate regions are tetraploid (Hagerup, 1933, Löve and Löve 1966). However, in other parts of the world, there is neither the clear cut morphological discontinuity between the races of *V. uliginosum* that occurs in Atlantic regions, nor is there a sizable body of chromosome data on which to attempt to base correlations. There is also evidence, discussed above, that there is a much greater degree of cytogenetic complexity in the *V. uliginosum* complex than has previously been recognized.

Essentially the entire range of morphological variation of the *V. uliginosum* complex can be observed in Alaskan material, but there is no firm evidence that either  $n=12$  diploids or  $n=24$  tetraploids occur there. Specimens which are morphologically indistinguishable from  $n=12$  Greenland material commonly have a chromosome count of approximately or exactly  $n=36$ .

Hagerup (1933) indicated that the size and wall thickness of pollen grains might be useful in distinguishing chromosome races of *V. uliginosum*. I studied this possibility in some detail, but found no evidence of any correlation between either wall thickness or tetrad size and level of ploidy. Studies in comparative size and distribution of stomates were also inconclusive.

After examining several hundred specimens, I am forced to conclude that there is no morphological feature or combination of features that can be correlated unequivocally with chromosome races of *V. uliginosum* on a holarctic basis. However, in some cases, a combination of morphological, distribution, and cytological evidence indicates that some races may be characterized, at least in parts of their range, by a particular chromosome number. In the following treatment of the taxonomy of *V. uliginosum*, chromosome numbers are attributed to the subspecies. This indicates that these numbers have been reported from specimens which, on the basis of morphology and/or distribution, are almost certainly members of that subspecies. However, there is no implication that the given number is the only number, or even the most common number, associated with the subspecies in question.

The degree to which chromosome data should be reflected in taxonomy has long been a subject of contention among plant taxonomists. The position adopted by Löve (1951) and others is that differences in chromosome number are certain indications of sterility barriers between closely related populations. Under a rigid application of the biological species concept, these populations would be considered to differ at the species level. Löve (1951) believes that

slight but perceptible morphological differences can usually be found between populations with differing chromosome numbers, and that populations with these characteristics should be recognized as species. Thus, Löve (1954) treats diploid members of the *V. uliginosum* complex as *V. gaultherioides* Bigelow. D. Löve and Boscaiu (1966), on the basis of the supposedly distinctive morphology of *V. gaultherioides*, indicate that the diploid race of the *V. uliginosum* complex is widely distributed in the mountains of Europe, although they cite no cytological data from the area to support their contention. Since some of the Alaskan material with high chromosome numbers is morphologically indistinguishable from  $n=12$  material from Atlantic regions, the dangers of extrapolations of this sort are obvious. Although there are probably intrinsic barriers to free interchange of genes between populations of *V. uliginosum* s. lat., lack of knowledge on the location and effectiveness of these barriers makes them useless for taxonomic purposes.

Several recent studies have produced compelling evidence that differences in chromosome numbers between closely related populations do not necessarily constitute insuperable barriers to gene exchange. It has been shown (Lewis, 1967, Marks, 1966) that gene exchange between diploid and tetraploid levels can take place through the production of reduced or doubled gametes, as well as through triploids. It has also been shown (Raven & Thompson, 1964; Dewet, 1965, 1968) that some polyploids may spontaneously revert to diploids. The previously mentioned work of Lewis (1970) indicates that chromosome numbers are not necessarily stable even over short periods of time, and that anomalous chromosome numbers do not necessarily interfere with normal meiosis.

It appears then, that the contention that differences in chromosome number are infallible guides to reproductive isolation and species delineation can no longer be supported either philosophically or theoretically. In *V. uliginosum*, there are no major morphological features that can reliably distinguish members of the various races of the complex



over a broad geographical or ecological range, and there is no sound basis for recognizing more than a single species within the complex.

#### SYSTEMATIC TREATMENT

The nomenclature used in the following systematic treatment is largely based on older literature in which type specimens were not designated. In other cases, the type specimens have been lost or are unavailable. The names are applied here on the basis of descriptions in the literature in conjunction with studies of more modern specimens collected at, or in the vicinity of the type localities.

#### *Key to the infraspecific taxa of Vaccinium uliginosum L.*

- a. Leaves pubescent. Diffuse, spreading, stoloniferous shrubs. .... 1. ssp. *pubescens*
- a. Leaves glabrous or faintly puberulent. Growth habit variable.
  - b. Dwarf, prostrate or matted shrubs; leaves usually less than 10 mm long; dead leaves often persistent on twigs for several years. .... 2. ssp. *gaultherioides*
  - b. Robust, often tall grown shrubs, usually of compact, shrubby growth habit.
    - c. Stomata present only on the lower surfaces of the leaves.
      - d. Common plant in many areas of northwestern North America and eastern Asia, occurring in a wide variety of habitats. Fruit variable in shape, often sub-cylindrical, highly palatable. .... 3. ssp. *pedris*
      - d. Plant of bogs and moorlands of Greenland and western and northern Europe. Fruits spherical, relatively insipid and tasteless. .... 4. ssp. *uliginosum*
- c. Stomates present on both surfaces of the leaves.
  - e. Plant of low, creeping habit. Leaves mucronate or cuspidate at the apex. Occurring in

- alpine situations along the coast of southern Alaska and the Aleutian Islands. ....  
 ..... 5a. ssp. *occidentale* var. *salicinum*  
 e. Plant of variable growth habit, usually erect. Leaf apex mucronulate, obtuse or rounded. Occurring in western North America from southeastern Alaska southward. ....  
 ..... 5b. ssp. *occidentale* var. *occidentale*

**Vaccinium uliginosum** L. Sp. pl. ed. 1: 350. 1753

1. **V. uliginosum** ssp. **pubescens** (Wormsk. ex Hornem.) comb. nov.

*V. pubescens* Wormsk. ex Hornem. Fl. Danicae: t. 1516. 1816.

*V. uliginosum* var. *pubescens* (Wormsk. ex Hornem.) Hornem. Nomencl. Fl. Danicae Emend. 73. 1827.

*V. uliginosum* var. *alpinum* Bigel. Fl. Bostoniensis ed. 2: 183. 1824.

*V. uliginosum* var. *Langeanum* Malte, Rhodora 36: 184. 1934.

*V. uliginosum* var. *alpinum* f. *Langeanum* (Malte) Polunin, Bull. Nat. Mus. Canada 92: 315. 1940.

*V. uliginosum* f. *pubescens* (Hornem.) Polunin, Bull. Nat. Mus. Canada 92: 315. 1940.

Diffuse, stoloniferous shrub, 1-3 dm tall. Leaves: elliptic or obovate, 10-25 mm long, more or less densely pubescent on both surfaces, apex obtuse, occasionally mucronulate. Flowers: borne singly or in racemes of two or three, 5(4)-merous, corolla white or pink, campanulate or urceolate. Anther horns long, divergent at the base, usually exceeding the tubules. Fruits spherical, 4-6 mm diam., sweet.

This is the most common subspecies of *V. uliginosum* in low arctic tundra and muskeg situations. Throughout most of central Canada and Siberia, this is the only race known to occur. In these areas, populations are uniform and usually densely pubescent. In central Alaska, this subspecies appears to intergrade with ssp. *pedris*, and there are populations there which are variable in terms of leaf pubescence.



Fig. 2. Range of *Vaccinium uliginosum* ssp. *pubescens*. Not included are a number of specimens from Siberia in which the exact collection locations were not given.

Subspecies *pubescens* is the only circumpolar race of *V. uliginosum* (Fig. 2). It is apparently rare in Greenland and northern Europe. Chromosome counts of  $n=24$  from New Hampshire (Löve and Löve, 1966) and Russia (Strelkova and Sokolovskaya, 1960) refer to ssp. *pubescens*.

2. *V. uliginosum* ssp. *gaultherioides* (Bigelow) comb. nov.  
*V. gaultherioides* Bigel. (pro parte), New Engl. Journ. Medic. & Surg. 5: 335. 1816.

- V. uliginosum* var. *gaultherioides* (Bigel.) Bigel.,  
(pro parte), Fl. Bostoniensis, ed. 2: 183. 1824.
- V. uliginosum* \**microphyllum* Lange, Meddel. om  
Grønl. 3: 91. 1880.
- V. microphyllum* (Lange) Hagerup ex A. Löve, Bot.  
Not. 103: 49. 1950.

Dwarf, tufted, matted, or procumbent subshrub. Main branches usually prostrate or semi-subterranean, thick, twisted, commonly bearing dense tufts of pale yellowish-brown adventitious twigs. Leaves 5-10 mm long elliptic or obovate, glabrous or with a few fine hairs on the petiole or lower leaf blade, apex obtuse or acute, occasionally mucronulate. Flowers borne singly on pedicels usually less than 2 mm long, 5(4)-merous, corolla pink or white, campanulate or urceolate. Anther horns long, divergent at the base, usually exceeding tubules. Fruits sparse, usually more or less spherical, 2-4 mm diam.

This subspecies is common in alpine and high arctic areas in Greenland, Iceland, eastern Canada, and alpine areas in New England.

Morphologically similar specimens also occur in northern Europe and arctic Alaska and western Canada (Fig. 3). It is not clear whether these specimens should be considered as ssp. *gaultherioides* or as alpine elements of ssp. *uliginosum* and ssp. *pedris*, respectively. All chromosome counts of  $n=12$  (see page 441) in *V. uliginosum* refer to ssp. *gaultherioides*.

3. *V. uliginosum* ssp. **pedris** (Harshberger) comb. nov.

*V. uliginosum* var. *pedris* Harshberger, Proc. Am.  
Phil. Soc. 67: 232. 1928.

Dense, compact, upright or spreading shrub. Leaves 10-30 mm long, elliptic, obovate or orbicular, glabrous, sometimes puberulent in the more northerly parts of the range; apex obtuse, rounded, truncate, or retuse, occasionally mucronulate. Flowers usually borne in racemes of 2 or 3, on pedicels 3-12 mm long, 5(3, 4)-merous, corolla white or

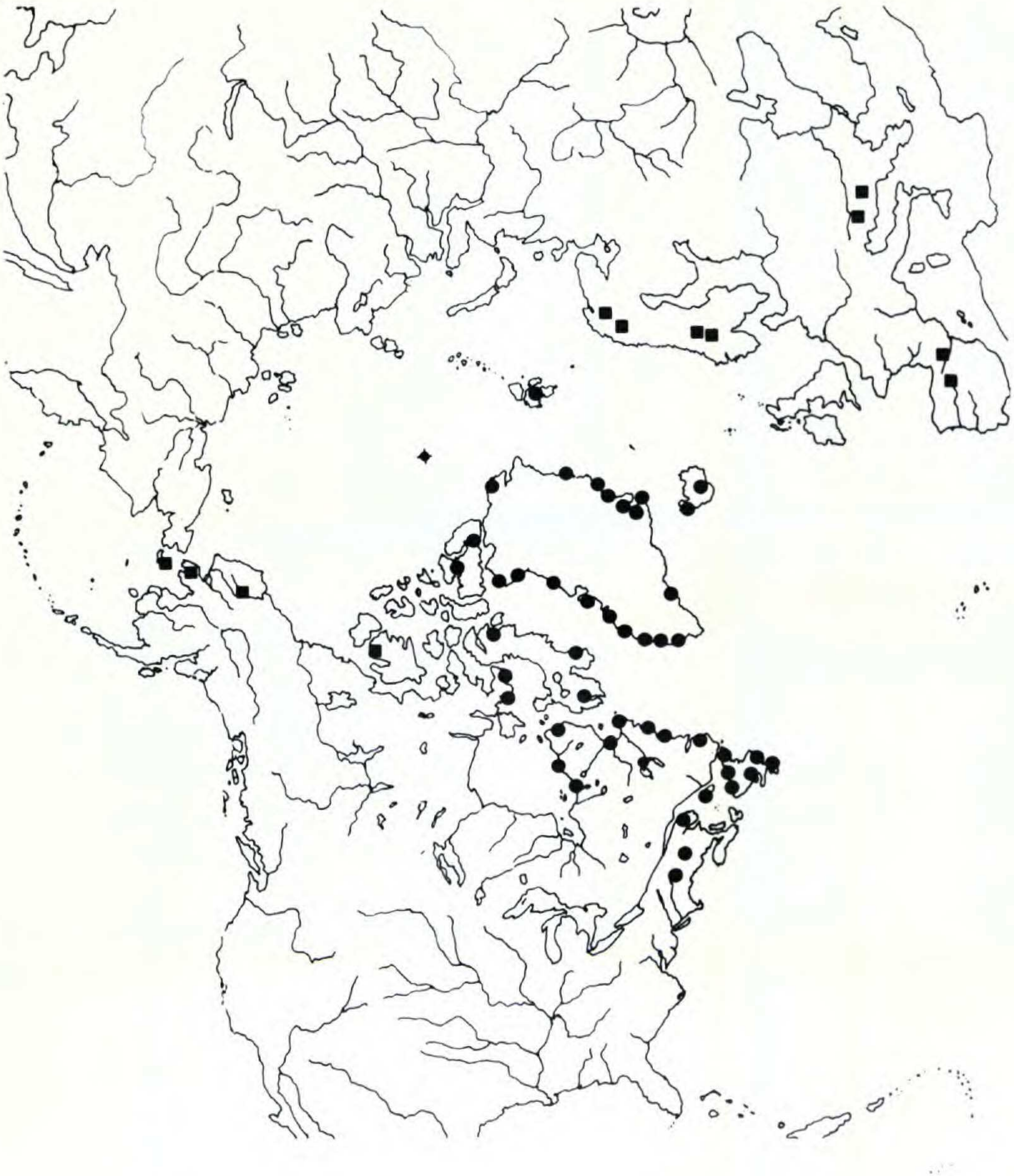


Fig. 3. Range of *Vaccinium uliginosum* ssp. *gaultherioides*. Squares indicate collection locations of specimens which seem morphologically to belong in this subspecies, but which may be derived from other subspecies.

pale pink, usually campanulate. Anther horns variable, most commonly short, ascending, occasionally obsolete or downward turning, occasionally long and divergent at the base. Fruits variable in shape and size, often subcylindrical or subglobose, abundant and sweet.

This subspecies occurs in a wide variety of habitats in northwestern North America and eastern Asia (Fig. 4). Specimens occurring in muskegs in central and northern Alaska sometimes have slightly pubescent leaves and a rather diffuse growth habit; this may be the result of intergradation with *ssp. pubescens*. Chromosome numbers:  $2n=72$  (Hara, 1953),  $n=36$  (in some cases) (Young, 1965, unpub.).

#### 4. *V. uliginosum* ssp. *uliginosum*

*V. uliginosum* L., Sp. pl. ed. 1. 350. 1753.

Erect or spreading shrub. Leaves 10-30 mm long, elliptic or obovate, apex rounded or obtuse; commonly thin and membranaceous, glabrous or occasionally (in northern Europe) slightly puberulent. Flowers usually borne in racemes of two or three on pedicels 3-10 mm long; 5(4)-merous, corolla white, usually campanulate. Anther horns variable,

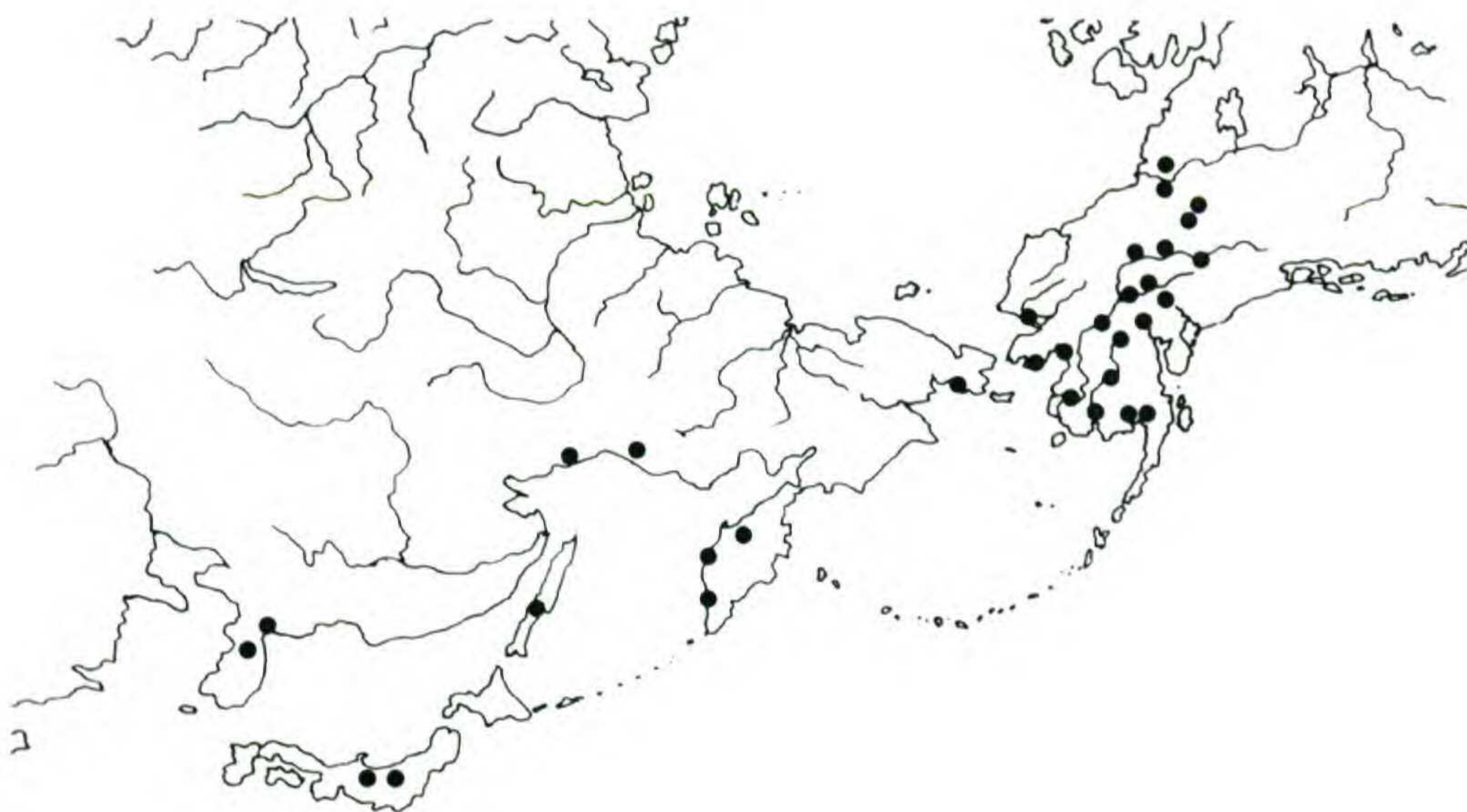


Fig. 4. Range of *Vaccinium uliginosum* ssp. *pedris*.



Fig. 5. Range of *Vaccinium uliginosum* ssp. *uliginosum*.

commonly short and ascending. Fruits spherical, 3-6 mm diam., insipid and not very palatable (Hagerup, 1933, Hultén, 1948).

A fastidious hydrophyte (Hagerup, 1933) occurring in bogs in northern Europe, Iceland, Greenland, and possibly in eastern North America (Fig. 5). Chromosomes:  $n=24$  (Hedberg and Hedberg, 1964, Hagerup, 1933).

5. ***V. uliginosum* ssp. *occidentale*** (A. Gray) Hultén, Ark. Bot. n.s. 7(1): 100. 1968.

Differs from all other subspecies of *V. uliginosum* by having stomates on both upper and lower surfaces of the leaf blade. Two varieties are known; these intergrade in a zone of contact in south central and southeastern Alaska, (Fig. 6).

5a. ***V. uliginosum* ssp. *occidentale* var. *salicinum*** (Cham.) Hultén, Fl. Aleutian Is. 268. 1937.

*V. salicinum* Chamisso, Linnaea 1: 525. 1826.

Robust but usually creeping or procumbent shrub. Leaves 5-25 mm long, elliptic, glabrous; apex cuspidate or mucro-

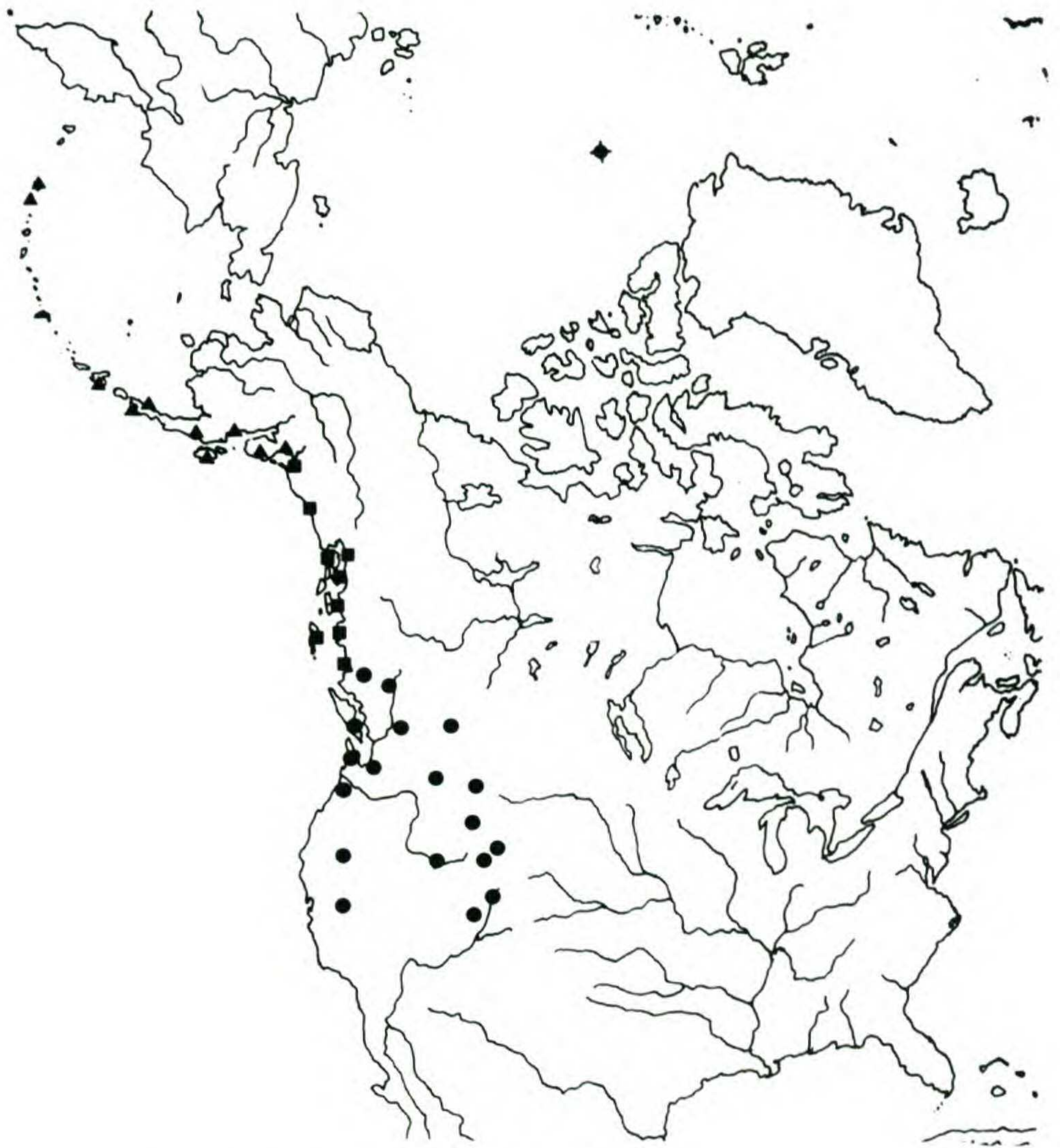


Fig. 6. Range of *Vaccinium uliginosum* ssp. *occidentale*. Triangles represent var. *salicinum*, dots var. *occidentale*, squares represent specimens which are intermediate between the two varieties.

nate. Flowers borne singly on short (less than 2 mm) pedicels, sometimes nearly sessile 5(6, 7)-merous, corolla red or pink, urceolate. Anther horns divergent, longer than tubules. Fruit spherical, 3-6 mm diam.

Occurs in alpine situations along the southern coastal border of Alaska westward to Attu Island.

5b. *V. uliginosum* ssp. **occidentale** var. **occidentale** (A. Gray) Hara, Journ. Jap. Bot. 28: 83. 1953.

*V. occidentale* A. Gray, Bot. Calif. i. 451. 1876.



Shrub of variable growth habit, usually erect, occasionally spreading in alpine or boggy habitats. Leaves 5-30 mm long, elliptic or obovate, glabrous; apex acute, obtuse or rounded, occasionally mucronulate in the more northern part of the range, where this variety intergrades with var. *salicinum*. Flowers borne singly or in racemes of two or three, length of pedicel variable 1-10 mm; 5(4) merous, corolla pink or white, campanulate or urceolate. Fruits spherical, 3-6 mm diam.

This variety is in many ways the southern counterpart of ssp. *pedris*, which it resembles morphologically in terms of its wide range of morphological variability. However, the fact that all specimens examined had stomata on the upper surfaces of the leaves, while no specimens of ssp. *pedris* showed this character, indicates that var. *occidentale* should be placed in the same subspecies as var. *salicinum*.

Chromosome counts of ssp. *occidentale* var. *salicinum* indicate a variable number, probably including  $n=36$ , and possibly  $n=18$  (Young, 1965, unpub.).

#### PHYTOGEOGRAPHICAL CONSIDERATIONS

The vast majority of the area presently inhabited by the various races of *V. uliginosum* was repeatedly covered by continental ice sheets during the Pleistocene. The only large unglaciated areas within the northern part of the present range of *V. uliginosum* are in central Alaska and Siberia (Flint, 1957). In southern Europe, western United States, and eastern Asia, the alpine habitats of *V. uliginosum* were glaciated, but populations could easily have persisted in the areas by means of relatively short altitudinal migrations. We may assume that populations of ssp. *pedris*, ssp. *occidentale*, and, perhaps to a lesser extent, ssp. *uliginosum* persisted in parts of their present ranges throughout the glacial maxima of the Pleistocene. These subspecies have extended their ranges considerably in postglacial times, but have only colonized the southern fringes of the Arctic. On the other hand, ssp. *pubescens* and ssp. *gaultherioides* have had immense migrations during postglacial times, and they

have colonized vast areas of the Arctic. Subspecies *pubescens* in particular seems to have great dispersal potential and excellent colonizing ability, as it has recolonized most of the deglaciated areas in the Arctic and subArctic in both hemispheres.

However, ssp. *pubescens* is not uniformly distributed over the entire arctic region. It is rare or absent in most of the more northern areas customarily referred to as the high Arctic. The varying role of ssp. *pubescens* in the composition of the tundra vegetation is strikingly apparent in northern Alaska. Subspecies *pubescens* (also ssp. *pedris*) is abundant in the northern foothills of the Brooks Range and throughout most of the interior portion of the Arctic Slope, but it is not known to occur along the arctic coast east of Cape Lisburne (Wiggins and Thomas, 1962). Thus there is a narrow belt of land some 500 miles long bordering the Arctic Ocean in northern Alaska in which *V. uliginosum* is not known to occur, although the species is common along the entire southern border of the belt. A similar situation exists in Canada and Siberia; in both cases, ssp. *pubescens* is rare or absent in the islands north of the mainland. In view of the high degree of vagility of ssp. *pubescens*, it must be considered that these northern areas are ecologically unsuitable for this subspecies. It is essentially a low Arctic plant.

Subspecies *gaultherioides* is not as vagile as ssp. *pubescens*, and its main area of colonization is in the Atlantic sector of the Arctic. However, ssp. *gaultherioides* has extended its range considerably beyond that of ssp. *pubescens* in the high Arctic. We can conclude that there are physiological differences between the subspecies which give them differing ability to live and reproduce under the extreme climatic conditions of the high Arctic. In high Arctic areas outside the range of ssp. *gaultherioides*, such as the Siberian Islands, *V. uliginosum* is not represented in the flora.

The history of ssp. *occidentale* seems to be closely intertwined with the glacial history of its range. The present status of this subspecies, with two varieties, can logically

be considered to be the result of at least two periods of glacial advance. Subspecies *occidentale* probably diverged from an ancestral population (ssp. *pedris*?) as a result of separation from the main population by glaciers. The significance of an increase in the number of stomates is not clear, but a correlation of this character with a humid climate is logical, since the number of stomates would have an effect on evapotranspiration. It is reasonable to propose the Pacific Northwest as the area of origin of ssp. *occidentale*. During a later interglacial, ssp. *occidentale* would have extended its range northward along the coast of Alaska, but not into the unsuitably dry environment of central Alaska. During the next period of glaciation, the northern populations of ssp. *occidentale* would have been confined to a few small refugia along the coast of southern Alaska (c.f. Karlstrom & Ball, 1969). These refugial populations would have been subjected to intense pressures by the worsening climate. The result would be the formation of the distinctive and relatively invariable race, var. *occidentale*. As the glaciers retreated once more, this race would have spread out of its relict areas and ultimately come into contact with populations of var. *occidentale* in the vicinity of southeastern Alaska, and hybridization would occur, blurring the lines between the races. There is also a broad zone of contact between the ranges of ssp. *occidentale* and ssp. *pedris*. However, the habitat requirements of these two subspecies are quite different ssp. *pedris* being a plant of muskeg and dry uplands, while ssp. *occidentale* occurs mainly in wet alpine areas. These differences in habitat requirements have probably been instrumental in keeping ssp. *pedris* and ssp. *occidentale* separate. The only area in which there is any evidence of intergradation between these varieties is in the vicinity of Bristol Bay, where an essentially "hybrid" environment prevails.

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